THE PES OF DIADECTES: NOTES ON THE PRIMITIVE TETRAPOD LIMB.

Par

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With 9 figures.

I. The Pes of Diadectes.

The foot of the diadectid reptiles is incompletely known despite the considerable amount of described material pertaining to the group. The greater part of the pes of *Diasparactus* has been described by CASE and WILLISTON[1]), but in *Diadectes* itself only isolated elements have been discovered[2]).

Material. The foot material described below belongs to a partial skeleton of *Diadectes* found by BRUCE N. CRANDALL and A. S. ROMER in 1928 near East Coffee Creek, Baylor, County, Texas, at a horizon about 50 feet above the Læuder's limestone, and hence at the very bottom of the Clear Fork, as that term is now used[3]). The remains are in general comparable with those of

[1]) Permo-Carboniferous Vertebrates from New Mexico, Carnegie Inst. Washington Publ. 181, Ch. IV, 1913.

[2]) CASE, E. C., Revision of the Cotylosauria. Carnegie Inst. Washington Publ. 145, 1911, pp. 82—83.

[3]) ROMER, A. S., Vertebrate Faunal Horizons in the Texas Red Beds. University Texas Bull. 2801, 1928, pp. 75—76. With regard to the vertical distribution of diadectid remains, Dr. CASE informs us that some years ago he saw a string of diadectid vertebrae in a private collection which had been obtained two miles west of Ringgold, Texas. This is at a horizon which Mr. F. B. PLUMMER informs us is about 600 feet below the top of the Cisco (Pennsylvanian), and about at the horizon of the Newcastle Coal. The specimen is of interest as being geologically by far the oldest of any vertebrate from the Texas Red Beds. It has since been destroyed by fire, and further search at the locality yielded only an indeterminate fragment.

D. phaseolinus as described by CASE[4]), and the size is similar (the femora average 20·6 cm. in length, as compared with 19 cm., the tibiae 12·9 cm. as compared with 13 cm. the fibulae average 14·9 cm. in length). Specific identity is improbable, as that species (and indeed, almost all described species of the genus) are from the Wichita group, considerably lower stratigraphically. Only two Clear Fork species have been described, *D. maximus*[5]) from some large dorsal vertebrae, and *D. huenei*[6]) from a skull of „normal" size. Direct comparison can not be made because of lack of homologous parts, and size alone is a poor criterion. In the circumstances, the present specimen is provisionally assigned to *D. maximus*, the first species described from the Clear Fork.

Fig. 1. Ventral view of the left pes of *Diadectes* as found. × 1/4.

The greater part of the left foot was removed in burlap without disturbing the original relations. A few phalanges are missing, and the first metacarpal was broken through. The pes as found (with the first digit restored to its original position) is shown in Figure 1. Most of the outer side of the right pes was recovered.

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[4]) CASE, E. C., op. cit., 1911, pp. 81—82.

[5]) CASE, E. C. New or Little Known Reptiles and Amphibians from the Permian (?) of Texas. Bull. Amer. Mus. Nat. Hist., 1910, XXVIII, pp. 174.

[6]) BROOM, R. Some Points in the Structure of the Diadectid Skull. Bull. Amer. Mus. Nat. Hist., XXXIII, 1914, p. 110.

Tarsus. Of the tarsus, there was found on the right side only the fibulare. On the left side, however, the entire tarsus was present, in nearly normal relations with the lower leg and digits.

The fibulare is irregularly triangular in shape. A considerable portion of its dorsal surface is occupied by a concave oval area with a „finished" surface of bone (i. e., smooth and not continued by cartilage). Dorsal and internal to this is a poorly ossified region with articular surfaces for the fibula and intermedium. The surface

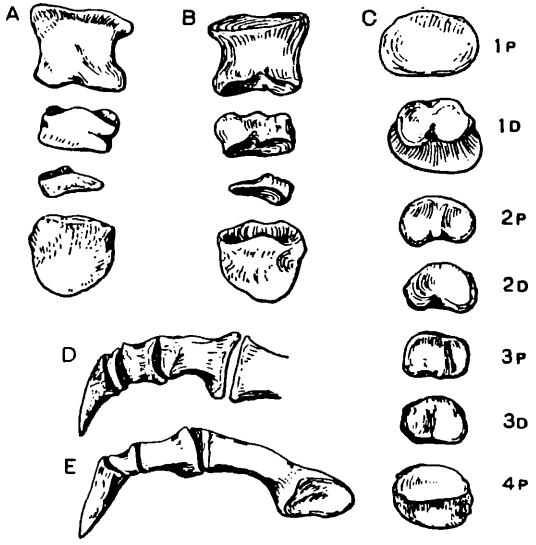

Fig. 2. Details of digits of diadectid foot. A. Phalanges of third toe of right pes, dorsal view. B. Same, ventral view. C. Proximal and distal articular surfaces of phalanges of third toe. D. Medial view of phalanges of third toe in natural articulation. E. Fifth toe, right pes, metatarsal and phalanges in natural articulation, medial view. All × 1/2.

for the former bone extends medially somewhat over onto the dorsal surface. This portion of the fibulare, because of the poor ossification, is somewhat irregular in outline, and is complete only on the left side: little of this area is present on the right fibulare. This area is also but little ossified in *Diasparactus*, as described by WILLISTON and CASE[7]), and appears to have been altogether absent in specimens of *Diadectes* described by CASE[8]), and by CASE and WILLISTON[9]). There is a thinner articular surface distally and medially

[7]) Op. cit., 1913, p. 29 and fig. 16.
[8]) Op. cit., 1911, fig. 31.
[9]) Op. cit., 1913, fig. 17.

for the external distal tarsals, and a smooth external margin. Ventrally there is a prominent transverse ridge crossing the bone; this, together with the dorsal concavity, inclines the distal portion of the fibulare forward at an angle of about 45° from the plane of the proximal portion.

The intermedium (astragulus) is preserved only on the left side. The bone is considerably crushed and somewhat imperfect, presumably owing to spongy texture and imperfect ossification. It had been displaced considerably downward and outward before burial. The element is about twice as broad as long, and rather thick. Proximally, there is a „finished" notch separating tibial and fibular articular surfaces. The fibular surface is a rectangular area which faces dorsally as much as proximally and appears to have supported the broad inner portion of the articular surface of the fibula. The tibial articulation is considerably larger than the fibular, but its surface is poorly preserved. It appears to have occupied a considerable area on the dorsal surface of the bone. These articular surfaces show that in life the plane of the astragulus would have been inclined considerably forward from that of the tibia and fibula.

A broad articular surface occupies the inner two-thirds of the distal margin; this was presumably in contact with the centrale. Laterally there is a broad surface for articulation with the fibulare. Between lateral and distal surfaces there is a deep and well-marked notch. Leading down to this on the ventral surface is a groove which narrows and deepens distally, and curves dorsally into the notch. This structure is similar to one which is found in *Seymouria*[10]) and *Limnoscelis*[11]), which WATSON has suggested to have been the arterial pathway which in higher reptiles is enclosed between intermedium and fibulare.

On the dorsal surface, as preserved, is a deep groove dividing the bone into inner and outer portions. It is tempting to believe that this represents a line of separation of fused intermedium and tibiale; but there is no trace of such a division on the well preserved ventral surface, and this groove may be partly, at least, of post-mortem origin. The intermedium figured by CASE and WILLIS-

[10]) WATSON, D. M. S., On *Seymouria*, the Most Primitive known Reptile. Proc. Zool. Soc. London, 1918, pp. 283—284, figs. 12, 13.

[11]) WILLISTON, S. W. Restoration of *Limnoscelis*, a Cotylosaur Reptile from New Mexico. Amer. Jour. Sci. 4th Ser. 34, fig. 20, 1913.

TON[12]) resembles our specimen except that the groove just mentioned is not present. The same is true of the intermedium of *Diadactes* figured by CASE[13]) and that of *Diasparactus* described by CASE and WILLISTON[14]).

But two distal tarsals are preserved, obviously the first and second. These are small, oval, imperfectly ossified nodules. The more external ones are not present (four were found in *Diasparactus)*; since, in the specimen, the intermedium was pushed down into the space which they should occupy, it appears that they were lost before burial.

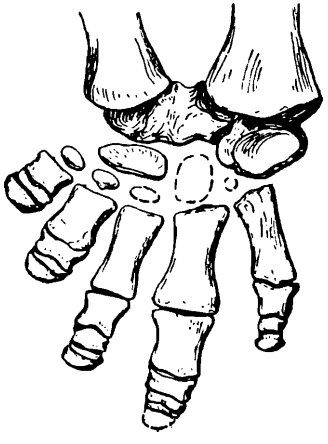

Fig. 3. Restoration of left pes, dorsal view. × 1/4.

One other bone is present in the tarsus. This was found close to the first distal tarsal. As preserved, it is a thin crescent, somewhat thickened on its straighter margin. Its dorsal surface is a „finished" one. It appears to have been a film of bone on the dorsal surface of a considerably thicker element. It seems to be a centrale, not previously reported in diadectids. (While we used this term, there is no evidence here to oppose the theory recently brought forward by BROOM[15]) that such an element may be a displaced tibiale.)

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[12]) Op. cit., 1913, fig. 17 C.

[13]) Op. cit., 1911, fig. 31. This is a left astragulus, seen from the ventral aspect, the proximal end at the right of the figure.

[14]) Op. cit., 1913, fig. 17, A, B. This is a right astragulus, not the left.

[15]) BROOM, R., On the Structure of the Reptilian Tarsus. Proc. Zool. Soc. London, 1921, pp. 143—155.

Digits. Between the two pedes, nearly the entire structure of the toes can be described. The first digit is preserved only in the left foot; the metatarsal is broken, and the tip of the end phalanx is missing. The second digit is complete on the left side. The third is complete except for most of the distal phalanx on the left, complete except for the metatarsal on the right. Except for the terminal phalanx, the fourth digit is complete on both sides. The fifth digit is complete on the right, but lacks the two distal phalanges on the left.

The lengths of the various elements (in many instances averages of two sides) are given below:

Digit	Mtt.	Ph. 1	Ph. 2	Ph. 3	Ph. 4	Ph. 5
I	15+	7	26±	—	—	—
II	30,5	13	7	24,5	—	—
III	36+	18	11	3,8	23	—
IV	48,5	32,5	14	8	4,5	?
V	38,5	14	8	21,5	—	—

Metatarsals. As would be expected, the metatarsals increase considerably in length from the first to the fourth with a decrease in the fifth. All except the last are comparatively short and broad. The bones are thin dorsoventrally, being about one-third as thick as broad in the middle of the shaft (there is some distortion, due to crushing). The ends broaden considerably. The ovaloid proximal articular surfaces appear to look slightly down as well as in. If the perpendicular to the distal articular surfaces of the metatarsals be taken as representing the general line of the digits, it will be found that the proximal articulation of the 5th metatarsal faces inward (proximally) from this at an angle of about 45 degrees (mainly owing to a curvature in the shaft of the bone); the fourth slants in the same direction at about 30 degrees; the second is nearly straight. (The remaining two are not well enough preserved for determination.) This suggests a configuration of the distal margin of the tarsus not very different from that actually found in the articulated left pes.

The distal articular surface of the long fourth metatarsal is a single elongate oval which presents a surface directed almost straight outward and lying in a plane perpendicular to the axis of the shaft. It shows only slight traces of a constriction in the center,

The third metatarsal is somewhat crushed but appears to have been essentially similar. The second, however, looks nearly as much down as distally, and is distinctly divided into two surfaces, with an especially deep notch in the center. The fifth is similar to the second.

The fifth metatarsal is remarkable for its comparative slimness and the great inclination of the head upon the distal part.

Phalanges. The phalangeal formula is obviously 2, 3, 4, 5, 3. The total length of the toes if extended (including metatarsals) would be approximately 58, 75, 93, 129 and 82 mm., respectively, showing the usual increase to the long fourth finger, with an abrupt drop to the fifth. The phalanges (usually broad) decrease rapidly in length towards the unguals, resulting in the presence, in the third and fourth toes, of penultimate phalanges consisting of thin plates of bone, three or four times as broad as long.

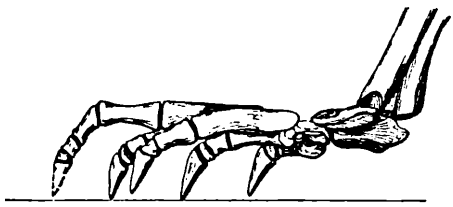

Fig. 4. Lateral view of restored left pes. × 1/4.

The terminal phalanges are, as has long been known, very hoof-like; they are very much longer than the joints immediately preceeding them. Their greatest width is not far from the proximal end; beyond, the distal and lateral borders form a smooth semi-ellipse. Thick proximally, the convex dorsal and flat ventral surfaces converge to meet at an angle of about 30 degrees at the distal end of the phalanx. The unguals undoubtedly were covered with a nail in life; the regularity of the distal margin suggests that this did not extend far beyond the termination of the phalanx; it may have been reflected back over the distal portion of the ventral margin.

Details of the structure of the phalanges may perhaps best be understood by taking such a digit as the third as typical.

The distal articular surface of the metatarsal appears to have been ovaloid, with little if any trace of division, looking almost directly outward in the line of the shaft. The proximal articulation

of the first phalanx was similarly shaped, with a height of about two-thirds of the width. Its plane is tilted slightly and shows that in life the phalanx was bent somewhat downward from the line of the metatarsal. The distal articulation, is directed about 20 degrees downward from the line of the shaft, and is divided into two surfaces by a deep ventral notch. These two surfaces face somewhat inward toward each other. The proximal articular surface of the second phalanx, although slightly imperfect, seems to have been applied fairly closely to the last; it is roughly saddle-shaped, divided into two portions facing slightly upward and somewhat outward. Ventrally, there appears to have been a small projection fitting into the notch on the first phalanx. The distal articular surface of this short joint faces again somewhat downward and is again partially constricted by a ventral notch.

The proximal articular surface of the very short third phalanx is somewhat concave dorsoventrally, with a slight dorsoventral median ridge which sends a ventral projection into the notch on the preceeding phalanx. This phalanx is thinner on the inner side with the result of throwing the tip of the toe slightly inward. The distal articular surface is not notched below, but is in surface view smoothly ovate, somewhat broader than high. Any one section is slightly convex dorsoventrally, concave in the other plane. The articular surface of the ungual is so tilted that the „hoof" is bent down sharply.

The tongue on the proximal ventral surface of the second and third phalanges appears to have afforded, as in modern lizards, a point of insertion for the main flexor tendon. In general, other tendonous insertions are not strongly emphasized. On the ungual there are apparent points of attachments on either side near the head.

If the metacarpal and phalanges be articulated in as nearly as possible the natural position, it will be seen that the phalanges curve downward strongly from the plane of the metacarpal, and that the flexed position of the toes was the normal one, as suggested by CASE and WILLISTON[18]) in the case of *Diasparactus*. The „hoofs" consequently cannot have rested on the surface of the ground, but must have approached a vertical position.

The other digits agree well, in general, with the structure outlined above. The joint between the ungual and penultimate phalanges

[18]) Op. cit., 1913, p. 24.

seems to have been the same throughout. A double articular surface with a tongue fitting a proximal ventral notch is consistently present in the next proximal joint, and apparently to some extent, at least, between all other segments of the digits except the metatarsal-first phalangeal joint of the third and fourth toes. In all the toes the downward curving of the phalanges seems to have been present; but in the third and fourth, the non-saddle-shaped proximal joint seems to have been fairly straight. This is obviously to be correlated with the greater length and greater number of phalanges of these toes in which the distal joints only would need to be curved, to give the proper alignment.

The fifth toe differs markedly from the others in a number of features, some of which have been noted above. It is comparatively shorter than in most primitive reptiles (it is 64 percent of the length of the fourth toe, as contrasted with 73 percent in *Ophiacodon*, for example). The toe is exceedingly slim as compared with the others; the metatarsal is curved, and there are only three phalanges in the articulated right toe, as compared with the four usually present in primitive reptiles. It is obvious that this digit has undergone considerable reduction. The reduction is not entirely confined to this toe; for the distal portion of the fourth toe appears to have been somewhat narrower than the inner ones.

This reduction is apparently usual in diadectids. For example, a bone figured by CASE[17]) is a fifth metatarsal of similar type. The pes of *Diasparactus* shows considerable reduction of the outer digits as well[18]). In addition, the outer toes of the manus of both *Diadectes*[19]) and *Diasparactus*[20]) appear to show some degree of reduction.

An apparent continuation of the same process of reduction is exhibited in the pareiasaurs, related large forms of later date. In these types the fifth digit in both manus and pes is tiny and may be altogether missing[21]).

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[17]) Op. cit., 1911, fig. 31, bone to the right of „a"

[18]) CASE and WILLISTON, Op. cit., 1913, fig. 16.

[19]) Cf. CASE, op. cit., 1911, plate 7, fig. 1.

[20]) Shown in the specimen, but not indicated in the somewhat diagrammatic figure of CASE and WILLISTON (1913, fig. 12).

[21]) BOONSTRA, L. D., Pareiasaurian Studies, III, IV, Ann So. Afri. Mus. XXVIII, 1929, pp. 97—122.

Restoration. From this material it has been possible to restore the foot with a fair approach to accuracy. When intermedium and fibulare are articulated, and tibia and fibula placed in their probable relative positions, a fair fit between foreleg and tarsus is obtained, although the imperfect nature of the proximal tarsal articulations (due to the presence of cartilage) renders exactness impossible. Arrived at independently, this articulation was found to agree with that in the specimen figured by CASE and WILLISTON[22]).

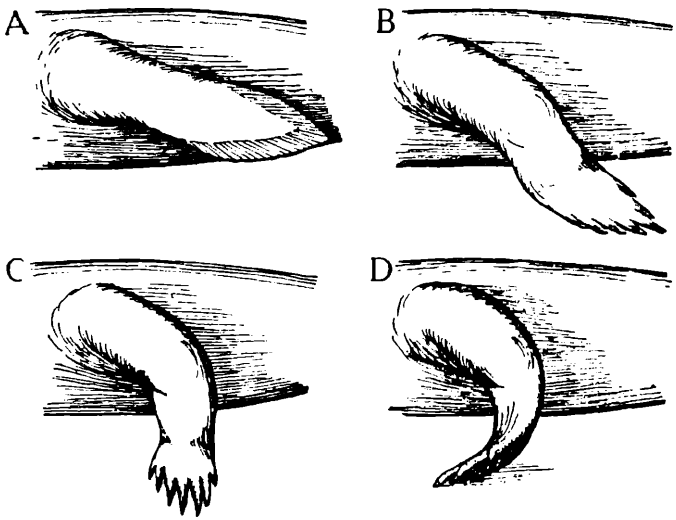

Fig. 5. Diagrams illustrating the probable changes in position during the evolution of a pelvic fin into a tetrapod pelvic limb. In A the fin is shown enlarged to tetrapod size, but in a position comparable to that found in *Ceratodus* and *Polypterus*, with the true dorsal surface turned outward and somewhat dorsally (cf. figure 7 B). A double flexure, creating knee and ankle joints would result in placing the limb on the ground, but with the foot directed backward (B). The proper orientation of the foot has been accomplished (C, D) by a marked rotation of the tarsal and digital region, which, it has been suggested, would account for many of the structures and structural tendencies seen in the primitive tetrapod pelvic limb.

Practically the entire distal surface of tibia and fibula are opposed by articular surfaces on the proximal tarsals. It seems probable, from the nature of these articulations, that considerable freedom of movement was present.

The dorsal as well as proximal position of the lower leg elements on the proximal tarsals, coupled with the angulation of the fibulare noted previously, tends to throw the plane of the tarsus forward from that of the lower leg at about a 45 degree angle.

[22]) Op. cit. 1913, fig. 11 C.

Beyond this, the lack of several of the more distal elements and the incomplete ossification of those present renders exact reconstruction of the more distal part of the tarsus out of the question. It is probable that the plane of the distal portion of the tarsus continued (approximately) that of the distal ends of the proximal tarsals. The position of the heads of the metatarsals can not be directly determined. The position found in the left foot seems to be a reasonable one, allowing for a slight spreading due to pressure during burial. This is checked by the angulation of the heads of the metatarsals, discussed previously. CASE and WILLISTON[23]) state that in *Diasparactus* „the foot was not set obliquely to the axis of the foreleg but was continued directly forward". We cannot confirm this in the present specimen and can not arrive at an articulation of the tarsus which does not incline the toes inward in rather normal reptilian fashion. As noted above, the fifth toe is divergent, a divergence which is partially „corrected" by the curvature of the shaft. This feature is, of course, present in most reptilian feet.

We have previously commented on the sharp downward curvature of the distal portions of the digits. It will be noted that the claws are directed downward at nearly a right angle to the line of the metatarsals (the digits were found articulated in very much this position). It is thus quite impossible to reconstruct the foot so that the digits will rest on the ground or so the under side of the „hoofs" will touch the surface, for while considerable extension and flexion of the toes was obviously possible (taking into account the well-developed articulations between the phalanges) it is impossible that they should ever be completely extended. The structure of the digits and the deduced position of the heads of the metatarsals suggests that the inner (tibial) side of the tarsus was lower than the outer. This is in agreement with the fact that the tibia is the main supporting element.

It seems most probable that the foot was covered below by a thick pad which would have enclosed not merely the tarsus but the portions of the digits which were not freely movable, and have extended to the end of the metatarsal in the case of the first, second and fifth toes, and to the end of the first phalanx in the case of the third and fourth. The freely movable portion of the toes would have extended outward and downward from the pad. A modern

[23]) Op. cit., 1913, p. 29.

analogy to this supposed construction is, as pointed out to us by Mr. KARL P. SCHMIDT, that of the manus of the large land tortoises. Not only are the two forms types with a somewhat similar gait, but in both cases we are dealing with animals which are the largest of their kind (the diadectids are the heaviest of Permo-Carboniferous reptiles). Again, the blunt claws of the land tortoises are used to some extent as digging organs; and in the case of the diadectids, while the early hypothesis that these creatures were burrowing types has long been abandoned, it is obvious that the toes were used in at least minor digging operations, in search of food more parti-

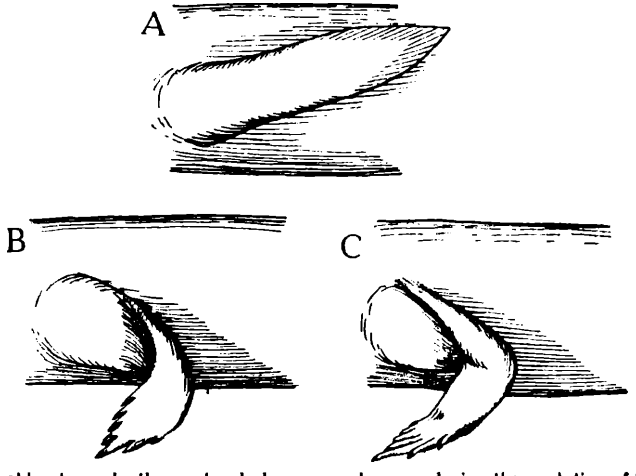

Fig. 6. Probable stages in the postural changes undergone during the evolution of the pectoral appendage, to be contrasted with figure 5. In A is shown the position assumed by the pectoral fin in such forms as *Ceratodus* and *Polypterus*. Here, in contrast with the pelvic fin, the ventral surface is turned outward, not inward, the preaxial margin is dorsal, not ventral, as in the pelvic fin (compare figures 7, 8). To bring the ventral surface in contact with the ground a sharp twisting of the entire limb is necessary (B), resulting in the tetrapod elbow joint. Once this has been accomplished, little further adjustment is necessary to bring the manus into its definitive position (C).

cularly[24]). The posture of the tortoise foot is quite similar to that postulated for Diadectes[25]).

NOPSCA[26]) has figured the footprint of *Korynichnium* as one which might be that of a diadectid type. But the only similar feature is the presence of blunt claws, and the long slim toes of that ichnite

[24]) CASE and WILLISTON, Op. cit., 1913, pp. 24

[25]) Cf. WILLISTON, S. W. Osteology of the Reptiles, fig. 115, 1925.

[26]) Die Familien der Reptilien, Fortschritte der Geol. u. Pal., Heft VI, Fig. 2, pp. 138—139 and 136, 1923.

are not all of an appropriate character. Much happier, we believe, is his suggestion that certain „stegocephaloid" footprints may be those of diadectids. From a consideration of the foot it would seem likely that the impression would consist principally of a large pad impression extending farthest proximally beneath the tibial region, and farthest distally under the fourth digit. Outside of this, and partially, if not completely isolated from the main pad, would be separate short digital impressions. Certain late Carboniferous and Permian ichnites are not so far in many respects from the type suggested. Especially close, apparently, is *Baropezia eakini*[27]) from the Grand Canyon; this is not improbably the track of a small diadectid.

II. Notes on the Early Stages of the Tetrapod Limb.

The reduction of the external digits seen in *Diadectes* and other early types calls to mind other tendencies commonly seen in the pelvic limb in early tetrapods, such as the reduction of the fibula with a correlated increase in the size of the tibia, and the loss or displacement of the tibiale and the consequent shortening of the tibial side of the tarsus. It appears possible that these and other features of the early chiropterygium may be accounted for by the mode of evolution of the tetrapod limb from the fish fin.

Our discussion of this process will be chiefly from a functional, rather than a purely morphological point of view, and the skeleton of the appendage will be considered mainly from the light which a study of the changes in function and position throws upon structural evolution. We shall at first confine our discussion tho the pelvic limb.

Position of the pelvic fin in bony fishes. The position of the fin in the tetrapod ancestor undoubtedly was similar to that shown in figures 5 A and 7 B. The fin was directed backwards, with the true dorsal (extensor) surface turned outward and

[27]) GILMORE, C. W. Fossil Footprints from the Grand Canyon. Smith. Misc. Coll. 77, pp. 18—23, 1926. These footprints are probably not assignable to *Trematops*, as GILMORE suggests, for it is highly improbable that this form or indeed any rachitomous amphibian had a five-toed manus. (Likewise, they do not belong to *Baropezia*, Carboniferous types of which some have tetradactyl manus.) They are almost certainly reptilian in character.

somewhat upward, the flexor surface inward; the preaxial margin (which later was to become distally the anterior and finally the inner margin) was at the ventral edge of the fin; the postaxial margin was at the dorsal edge.

This is essentially the position assumed by the pelvic fin of *Polypterus* and *Ceratodus;* the diagrammatic appendage figured differs in that it is shown enlarged to „pre-tetrapod" size for readier comparison. The fins of primitive actinopterygians are comparable in position, but tend to have the two surfaces in a more horizontal plane.

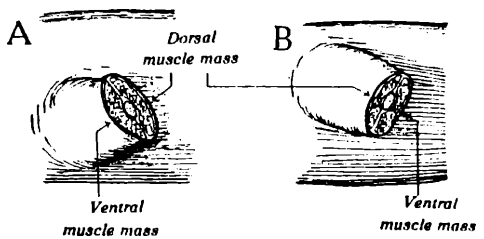

Fig. 7. Diagrammatic section to illustrate the contrast in posture between the pectoral and pelvic fins in fish. A. Pectoral fin, to be compared with figure 6A. The position of the ventral (flexor) and dorsal (extensor) muscle masses is indicated; the demarcation between them represents the plane of the fin. The preaxial margin is (roughly) dorsal, the postaxial nearly ventral in position. B shows the contrasted position of the pelvic fin (compare figure 5A).

First stages in the transition. For such a fin to gain a contact with the ground was a comparatively simple matter. The fin need but be directed slightly outwards from the body and tilted so that the preaxial edge is turned more laterally, and the extensor surface turned somewhat more dorsally. (Compare the living *Ceratodus.*) In this position, a slight downward bend near the middle of its length (the beginning of the knee joint) would result in the distal portion touching the ground; another flexure here (in the future tarsal region) would permit the distal portion (the pes) to touch the ground. (Figure 5 B.)

That some such primitive position once existed is strongly suggested by the conditions found in most Permo-Carboniferous tetrapods. In these forms, as noted by GREGORY and CAMP[28]) the femur is still directed somewhat posteriorly in its „average" position. The

[28]) GREGORY, W. K., and CAMP, C. L., Studies in comparative myology and osteology. Bull. Amer. Mus. Nat. Hist. XXXVIII, 1918, fig. 10.

original tilted position of the fin is still reflected in the musculature in lower tetrapods (Figure 8 B); the dorsal (exterior) muscles being situated somewhat to the front and outside of the pelvis and thigh, the ventral (flexor) muscles somewhat to the back and inside.

Rotation of the pes. It will be noted, however, that in such a position the developing foot is pointed outward and backward. Even in Permo-Carboniferous forms the tendency is to mount the limbs in this fashion, with the feet pointing outward, or even somewhat posteriorly[20]). But as is clearly shown by footprints, the feet point forward not only in tetrapods of this period, but even in older Carboniferous types.

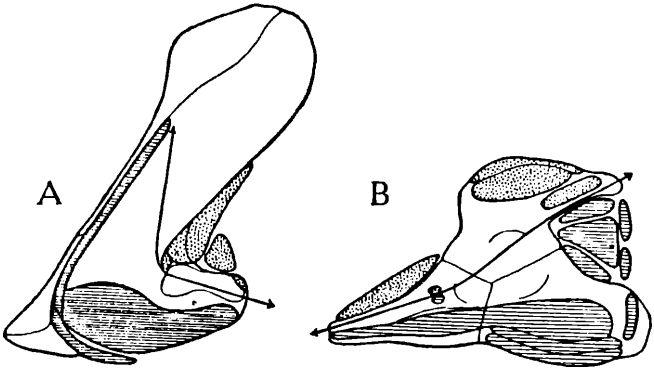

Fig. 8. Diagram of the shoulder (A) and pelvic region (B) of an early tetrapod, to show the retention, to a considerable degree, of the primitive position of the limb musculature. A may be compared with figure 7 A. The dorsal musculature (stippled) lies mainly posteriorly and internally as well as dorsally; the ventral musculature (hatched) lies ventrally and anteriorly. The heavy line separating the two groups represents roughly a projection of the plane in which the fin projected from the body. B shows the contrasted position in the pelvic fin (compare figure 7 B). (A, essentially *Eryops;* B, *Dimetrodon*).

Our problem, then, is to rotate the foot into its proper position with the toes pointing forward. The most probable a priori „solution" would be by a rotation of the entire limb, bringing the femur around to a position in which its distal end was anterior to the acetabulum; this would immediately bring the foot into line. This position was assumed later in mammal-like reptiles, mammals, some archosaurians, and birds. But as noted above, the fact is that

[20]) Cf., for example, WILLISTON, S. W., Osteology of the Reptiles, figs. 164, 167, 168, 169 A (1925).

in Permo-Carboniferous forms no such rotation had as yet taken place to any great degree[30]).

A second „solution" would be a rotation of the foreleg on the femur, so that the dorsal (extensor) surface would look anteriorly and dorsally rather than externally and dorsally. Such a rotation has seemingly taken place in the pectoral appendage where we find a sharp change of direction and considerable freedom of motion at the elbow. No such change, as is well known, has ever taken place at the knee; in almost all tetrapods the two principal segments of the hind leg have the simple relations of the two portions of a hinge.

It is thus obvious that the placing of the foot in a true tetrapod position depends almost entirely on a sharp twisting of the foot on the foreleg. This process (accompanied by a slight alteration in the position of the limb as a whole) is shown in Figure 5 C–5 D.

Results of rotation of the pes. Some of the results are obvious from the figure; they are still more obvious if the process be followed through in a two-dimensional paper model of the limb. The inner (preaxial) margin of the tarsal region should be shortened; the outer (postaxial) margin turns in a curve in such a fashion that the outer side of the tarsal region is lifted from the ground.

The inner side of the foreleg comes to bear most of the weight, since it is more directly under the femur and is alone in firm contact with the ground; the well-known tendency towards reduction of the fibula and increase in size of the tibia which seems to result from this is already under way in the more advanced Permo-Carboniferous types.

The necessary shortening of the inner side of the tarsus seems to have been effected by the reduction and disappearance or shif-

[30]) Mr. CHARLES R. KNIGHT has pointed out to us that the posterior position of the primitive knee gives it, alone, among tetrapods, the appearance of a „second elbow". In many restorations the foreleg is shown turned sharply and almost horizontally back from the femur, giving a more knee-like appearance (compare, for example, certain of the restorations in E. C. CASE, Permo-Carboniferous Red-beds of North America and Their Vertebrate Fauna, Carnegie Inst. Washington, Publ. 207, Ch. VIII, 1915). This, however, is based merely on a supposed analogy with the lizards, and I am unable to reconcile such a pose with any reasonable interpretation of primitive tetrapod limb movements.

ting of the tibiale which has been accomplished in almost every reptile.

Effect of foot rotation on the digits. Finally, the resultant position of the foot suggests the origin of the plan of the digits found in tetrapods in general, and of the peculiarities found in *Diadectes* and certain other types.

It is often assumed not only that the tetrapod foot has been derived from an „abbreviated archipterygial" type of fin, but that the structure was originally such that the axis ran through the fourth digit and that preaxial radials (prehallux, and first three digits) were more numerous than postaxial (fifth digit and postminimus). This may have been the case; but even if postaxial radials had been more numerous or the symmetry less marked it seems probable that the mechanics of the situation would have demanded a result similar to that which we find in the actual tetrapod foot[31]).

The rotation of the foot, as noted above, required that the outer side be elevated, the inner side depressed. This would cause a tilting in the plane of the pes, the plane dipping inwardly distally; consequently the intersection of this plane with the ground, the „strike", would extend diagonally forward and outward. If we assume the digits to have been (roughly) in line with the foreleg it is obvious that the inmost (prehallux or hallux) would have touched the ground nearest the tarsus and consequently would have been the shortest, and that following digits (as is actually the case) would have increased regularly in length. At some point (the fourth digit) a maximum length for an „efficient" toe would have been reached.

Beyond this point any more posterior and external radials which may have been present originally would have become, for the most part, useless. It might be possible for a digit to depart from the plane of the others and to reach the ground at the outer side. This apparently has been the case in many reptilian groups; the divergent fifth digit of lizards, etc., is well known. Unless such a divergence took place a fifth digit would tend to become non-functional and reduction (as in the case of *Diadectes*) would seem a logical consequence. (As previously noted, the fifth toe of *Diadectes* was somewhat divergent, as well.)

[31]) Broom (On the Origin of the Chiropterygium. Bull. Amer. Mus. Nat. Hist. XXXII, pp. 459—464, 1913) has made suggestions of a character functionally similar to those advanced below.

The fifth toe was not reduced in most other early reptilian types. Considerations of size and weight, however, must enter heavily into the mechanical problems of support; in larger forms the problems would be accentuated. *Diadectes* and its relatives were the largest cotylosaurs of that date and it would be in these forms that we might expect to find the greatest divergence from the general type. The still larger and later pareiasaurs, as we have noted previously, have continued this process of reduction.

The majority of the archosaurians have lost the fifth digit. But here the process appears to have been different. In their ancestors it is probable that the fifth finger had assumed a divergent position. Following this, the elongation of the metatarsals which usually took place in this group would find this digit too far removed from the general plane of the others to render it possible for it to function. (This process is quite analogous to the early reduction of the divergent pollex in ungulate mammals.)

In the more generalized mammals and mammal-like reptiles, there is no reduction of the fifth digit; the digits, with the exception of the hallux, tend to be subequal in length, and with a reduction of the number of phalanges to the same number. The reason for this appears to be the fact that here the rotation of the femur to an anterior position has taken place, so that the pes is no longer twisted on the foreleg; its plane tilts directly forward, and the „strike" of the plane of the foot is essentially transverse rather than diagonal, tending to equalization in finger length.

Tibial-astragular articulation. A further feature of the tetrapod pes is the development of a rolling surface on the intermedium for the distal end of the tibia (no such articulation is developed in the front foot). Apparently this process is but beginning in such a primitive type as *Diadectes*, but is well developed already in the contemporary pelycosaurs. We have previously treated the limb as if the relations of foreleg and pes were fixed, and considered only the „average" position. When the limb is advanced (at the beginning of a stroke), with the femur in its most anterior position, the twisting of the plane of the foreleg on the plane of the foot is less than that previously assumed; but at the end of the stroke, with the femur far back, the degree of torsion is extreme. The development of some sort of rolling surface to „take up" the effect of this change of position is almost a necessity

Comparison with pectoral limb. It is of interest to compare the conditions in the posterior extremity with those in the pectoral limb. Certain of the conditions postulated for the digits seem to hold true as illustrated by the fact that the fifth digit of the manus is lost in almost every known amphibian[32]). The contrasts are marked, however. (1) There is a sharp change of plane between the dorsal surface of the humerus and that of the forearm, while in the hind leg, the plane of the foreleg continues that of the thigh. (2) In the arm, muscular mechanisms for extension of the forearm are more powerful; in the leg, primitive adaptations are more for flexion of the distal segment. (3) There is no development of a rolling joint at the lower end of the radius, in contrast with the tibial conditions. (4) The radiale is retained while the corresponding tibiale is lost or displaced.

These marked contrasts may reasonably be assumed to have originated in a different evolutionary history; and these evolutionary differences are not improbably due to the radically different position of the pectoral fin of the primitive fish ancestor.

Contrast in fin position. The position of the pectoral fin in the forms from which tetrapods are presumed to have arisen is essentially that shown in figures 6 A, 7 A. Superficially it appears to resemble the pelvic fin shown in figure 5 A in its position. We have again a fin which (in *Polypterys*, *Ceratodus* etc.) is in a nearly vertical plane. It seems at first glance reasonable to assume that the outer surface, again, is the dorsal (exterior) one, and the inner the ventral (flexor) surface; that the upper margin of the fin is the preaxial border, the lower the postaxial. Upon this basis have been erected almost all theories of the derivation of the tetrapod limb skeleton, such as those of KLAATSCH, BROOM, GREGORY and WATSON. These writers have assumed, for example, that the ulna and the minimus digit have been derived from skeletal elements which lie towards the upper margin of the fin, the radius and pollex from elements nearer the ventral margin (Figure 9 A).

[32]) Cf. GREGORY, W. K., R. W. MINER and G. K. NOBLE, the Carpus of *Eryops* and the Structure of the Primitive Chiropterygium. Bull. Amer. Mus. Nat. Hist., XLVIII, pp. 279—288, 1923. It now seems assured that the missing digit is the fifth, not the first.

These theories, however, are based upon a fundamental fallacy. Braus[33]) long ago pointed out that the outer side of the fin is not the dorsal surface but the ventral (flexor) surface, and one of us (A. S. R.) has confirmed his conclusions[34]). As shown by both innervation and relations to the shoulder girdle, the musculature of the outer surface of the fish pectoral fin pertains to the ventral (flexor) group, the musculature of the inner surface to the dorsal

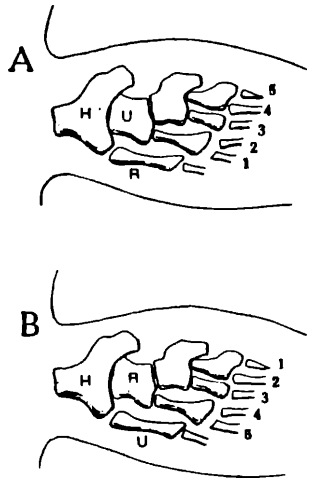

Fig. 9. A. Usual interpretation of the orientation of the crossopterygian pectoral fin, and identification of skeletal elements (simplified after Gregory, 1928). B. Correct interpretation. H, humerus; R, radius; U, ulna; 1, 2, 3, 4, 5, assumed order of digits.

(extensor) group. In consequence it is obvious that the seeming similarity in position between pectoral and pelvic fins is fallacious (Figure 7). In the pectoral fin it is the preaxial margin which is dorsal, the postaxial ventral, not the reverse.

This contrasted position is still reflected in the relation of the musculature to the girdles in lower tetrapods (Figure 8). While in the pelvic limb the ventral musculature originates mainly from the posterior part of the pelvic region, in the pectoral limb the reverse is true. The line of demarcation between muscle groups still represents roughly the plane in which the fish fin sprang from the body

[33]) Braus, H., 1901. Die Muskeln und Nerven der Ceratodusflosse. Semon's Zool. Forschungsreisen, Bd. I, II. Lief., 137—300.

[34]) Romer, A. S., Pectoral Limb Musculature and Shoulder-girdle Structure in Fish and Tetrapods. Anat. Rec., 1921, pp. 119—143.

Stages in change of pectoral limb posture. It has usually been assumed that the pectoral fin, in its change into a tetrapod appendage, followed much the same evolutionary course as we have indicated for the pelvic. On such a basis the contrasting structural differences are difficult to explain. But when it is recognized that the two fins were oriented in a very different manner, it is obvious that the evolutionary processes must have differed radically in the two cases, and that (as is the case) different structural features might appear in the end result.

The obvious steps in the assumption of the tetrapod pose of the pectoral appendage must have been similar to those indicated in Figure 6. The fin must be sharply twisted over so that the distal dorsal surface, which originally faced inward, now faces out and down, and perhaps somewhat anteriorly; this twisting brings the primitive elbow joint into existence. With the bringing of the distal portion into contact with the ground, the separation of pes and forearm is accomplished.

The sharp twisting appears to furnish the explanation of the marked contrast of the elbow joint with the knee joint. The greater freedom of motion of the former, the change of plane of the forearm from that of the humerus (as contrasted with conditions in the hind leg) and the rotational power (absent in the hind leg) all seem to have had their origin in this process which would seem at first sight to have been an awkward one, but which, once accomplished, appears to have enabled the pectoral limb to reach tetrapod conditions with comparatively little change. For, since the plane of the forearm is twisted upon that of the humerus, the pes, if extended directly from it without rotation, would point somewhat anteriorly as well as outwardly from the very first, and hence only a comparatively small degree of twisting would be necessary to bring it into an anteriorly-pointing position.

The manus. That some twisting is necessary seems fairly obvious. Its results seem to be shown in the digits, in which the arrangement is similar to that in the hind leg; it is probable that the same mechanical factors are involved. Further, there are similar tendencies for specialization and reduction of the fifth toe. This toe is lost in all amphibians except the earliest; it is somewhat reduced in diadectids, and may be entirely lost in pareiasaurs.

The lessened amount of twisting, coupled with the rotational powers present in the forearm (in contrast with the lower leg) seem to have resulted in the retention of primitive conditions in the relations of radius and manus. The results of twisting seem to have been „taken up" in the digits and there has been no necessity for reduction on the inner side of the podial region, and (whereas the tibiale is lost) the radiale has been retained. Further, the rotational power of the elbow joint seems to have rendered a rolling joint, of the type necessary in the stiffer posterior leg, unnecessary in the case of the radial-carpal articulation.

Principal motion. In the case of the hind leg, it is probable that the distal segment was primitively flexed on the femur during the „stroke" of the limb. That this was the principal action is suggested by the fact that the flexor muscles to the lower leg are highly developed in all known tetrapods, while the extensor muscles (triceps) appear to have been comparatively weak at first; the femoro-tibialis (vastus) appears only in amniotes.

It has been assumed that, in primitive forms the principal motion at the elbow was one of flexion[35]). While it is not feasible here to enter into a discussion of the question, there is evidence suggesting that the reverse was true, for the principal muscle used for this purpose, the biceps, is not present in amphibians at all, and only develops in reptilian types, where it is obviously a neomorph, perhaps composite in origin[36]).

Homologies of pectoral limb skeletal elements. It results from what has been said above that current theories regarding the origin of the tetrapod pectoral limb from the crossopterygian fin are erroneous in their interpretation of elements and regions. The homologue of the ulna must be towards the apparent lower edge of the fin (not the upper) since this is the postaxial margin; the homologue of the pollex from some element near the upper edge of the fin (not the lower) since this is preaxial ect. (Figure 9). We can supply no picture which satisfactorily replaces this incorrect interpretation. However, it may be pointed out that (1) our knowledge of crossopterygian fin structure is

[35]) Watson, D. M. S., 1917. The evolution of the tetrapod shoulder girdle and fore limb. Jour. Anat., LII, pp. 13—14.

[36]) Romer, A. S., The locomotor apparatus of certain primitive and mammal-like reptiles. Bull. Amer. Mus. Nat. Hist. XLVI., 1922. p. 563.

still extremely limited, while those types which are known exhibit considerable variation, so that comparisons must be regarded as highly speculative in any case, (2) as has been noted previously, the symmetrical arrangement (of the digits especially) would for the most part be a logical result of the mechanical necessities of the case.

GREGORY[37]), alone among recent writers on this subject, has admitted the possibility that the rotation of the pectoral limb may have taken place as we have outlined (his figure 8, a). His treatment, however, takes the opposite viewpoint. His argument for this is the direct comparison of the amphibian and crossopterygian limb skeletons. The validity of this comparison, however, is a point in question, and can hardly be used in its own proof. He suggests that embryological evidence as to musculature in lower tetrapods may be decisive.

One of us (A. S. R.) has studied the musculature of lizards with this point of view in mind. The work has not yet been completed, but the results, in correlation with embryological work on fishes by various writers, show the following, with regard to the pectoral appendage:

1. The ventral (flexor) musculature of lizards including that of the palmar surface of the manus, is homologous with the ventral musculature which lies on the under side of the fin of such a form as the elasmobranchs.

2. SEMON[38]) has shown that the musculature of the outer surface of the *Ceratodus* fin is homologous with the ventral surface of the elasmobranch fin.

3. Hence the outer surface of the pectoral fin of such a form as *Ceratodus* is homologous with the flexor and palmar aspect of the tetrapod limb.

For the pelvic fin it seems similarly assured that the ventral and plantar aspect of the tetrapod limb is homologous to the ventral surface of the elasmobranch fin and to the median surface of the *Ceratodus* fin.

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[37]) GREGORY, W. K., The Upright Posture of Man. Proc. Amer. Philos. Soc. LXVII, pp. 339—376, 1928.

[38]) SEMON, R., Die Entwicklung der paarigen Flossen des *Ceratodus forsteri*. Semon's Zool. Forschungsreisen, Bd. I, 59—111, 1898.

It will be noted that we imply no condition of „reversed symmetry" in the two limbs. In the arm, the original ventral aspect had tended to become lateral, but in tetrapods reverted, distally at least, to its primitive ventral (and palmar) position. In the hind leg, the ventral surface had moved medially, but in the transition to the tetrapod became again ventral (and plantar).

Summary.

1. The pes of the Permian reptile *Diadectes* is described and restored.

2. Many features of the structure and evolutionary trends of the tetrapod limb skeleton may be interpreted as resulting from the mechanical situation consequent upon its evolution from the fish fin.

3. The structural differences between pectoral and pelvic limbs may be interpreted as due to the fundamentally different posture of the pectoral and pelvic fins in the fish ancestors.

4. Current comparisons of the skeletons of tetrapod pectoral limbs and fish pectoral fins are erroneous, for the true position of the fish fin is the reverse of that assumed.